SYNOPSIS

In societies where all individuals are reproductively totipotent and yet, at a given time only one of them reproduces, it is interesting to examine the factor(s) that may influence and predict who will be the reproductive. I am investigating various behavioural, morphological and physiological parameters in the primitively eusocial wasp *Ropalidia marginata*, and their role in determining the current reproductive and her future successors. In several group-living species, especially in primitively eusocial ones, a strong link between behavioural dominance and reproductive dominance is observed. Hence, I am also investigating the possible determinants of behavioural dominance in *R. marginata*. I have carried out my study on artificially constituted pairs of wasps as well as in natural colonies in laboratory cages, which represent the founding phase and the established phase in the colony cycle, respectively.

Chapter 1: Behavioural and Reproductive Dominance in Pairs of *R. marginata*

Age and body size had no effect on behavioural dominance in pairs of *R. marginata*, whereas prior experience of behavioural dominance affected future dominance status, indicating presence of winner- and loser-effects. Dominance ranks are relatively stable. This is different from what has been found in colonies, where dominance ranks sometimes change on a daily basis.

Body size had no effect, whereas age and behavioural dominance had a significant effect on reproductive dominance in pairs, with older individuals and

more dominant individuals having a higher probability of becoming the reproductive. Since no relationship was found between age and behavioural dominance, we predict that the underlying mechanisms by which age and behavioural dominance affect reproductive dominance and independent of each other. This study gives a clear indication that age and behavioural dominance are important variables that determine the reproductive individual during the founding phase of the colony.

Chapter 2: Comparison of Dominance Indices and Recommendations for their Use

When several individuals interact with each other as in colonies, in a differential and sometimes in a preferential manner, it is difficult to attribute dominance ranks to individuals. Dominance indices are employed to simplify these interactions and rank individuals in dominance hierarchies. Since the rationale behind using a particular dominance index is seldom given in behavioural literature, a comparison of three dominance indices was carried out in second part of the thesis. Each index was gauged on how similar are its ranks as compared to other two indices. Indices were also compared based on the number of untied or unique ranks they attributed. The index that gave least number of ties in ranks was assumed to be better than others. In addition to data from *R. marginata* colonies, I used data from *R. cyathiformis* colonies (a congeneric species which behaves more like a typical primitively eusocial species), and artificial data sets, to increase variability in the interaction patterns. We found that each of the indices had their own advantages and disadvantages. In species like *R. marginata*

and *R. cyathiformis*, where only a few pairs show interactions, and among those who do, very few show reversals, Frequency-based Dominance Index (FDI) is the recommended index of choice. Studies like these will help in understanding how dominance indices operate under certain situations before applying them to construct hierarchies.

Chapter 3: Behavioural and Reproductive Dominance in Colonies of *R. marginata*

Age does not affect behavioural dominance, whereas winner and loser effects exist in colonies of *R. marginata*, just as in pairs. When analysed in detail, I found that colonies of *R. marginata* showed fewer proportion of pairs interacting, and lower frequency/hour/pair of dominance-subordinate interactions as compared to experimentally paired individuals (from 1st chapter). However, the dominance displays and behaviours were much more intense and severe in colonies. After dominance hierarchies are already established in colonies, frequent need to show dominance behaviour may not arise, due to familiarity between interacting individuals. However, since individuals are possibly aware of each others' strengths due to past interactions, dominance behaviours are much more severe when contests do happen. My results show that there might be some similarities in terms of determinants of behavioural dominance between pairs and colonies, but the expression of behavioural dominance is quite different.

From earlier work it was already known that if the queen/reproductive of the colony disappears or is experimentally removed, one of the individuals shows extreme levels of aggression. This individual, referred to as the potential queen

(PQ), will go on to become the next queen of the colony. Her behavioural profile, from the emergence till she establishes herself as the next queen have been well studied earlier. What was not known were the factor(s) that determine the identity of the PQ. It was also unclear what happens when the queen as well as the PQ are both removed, simultaneously or in quick succession. To test whether there is a longer reproductive hierarchy in *R. marginata*, the queen and the first potential queen of a nest were removed. I found that successive potential queens emerged as readily as the first potential queen, and with dominance profiles comparable to the first PQ, indicating that a reproductive hierarchy indeed exists, at least up to five PQ's. It was also found that these potential queens were acceptable to all other individuals, as there was not a single act of behavioural dominance directed toward any potential queen. It was also observed that all PQs went on to become queens if the previous queen or PQ was not returned. When tested for various morphological, physiological, behavioural and life history traits (factors possibly influencing the position of an individual in the reproductive hierarchy), we found that age is the only variable that emerges as an important predictor of reproductive succession, with older animals having a higher chance to succeed as next queens of the colony, although even age is not an absolute predictor. Unlike in the pairs, in colonies of *R. marginata* behavioural dominance is not a good predictor of an individual's ability to be the queen or the potential queens.

The four most important findings of my study are: (i) the first demonstration of winner and loser effects in social insects; (ii) the demonstration that behavioural dominance influences reproductive dominance in pairs but not in colonies; (iii)

demonstration of a long reproductive queue among individuals of a colony; and (iv) discovering that age is an important predictor of the identity of the queen and the future queens of the colony. I believe these findings will add significantly to our growing knowledge of the social biology of *R. marginata*.

Finally, my work shows that pairs of *R. marginata*, representing the founding phase of the colony, behave more like a typical primitively eusocial species, whereas colonies which represent the established phase of the colony cycle behave more like highly eusocial species. Finding the characters of two different forms of sociality in the same species in different phases of the colony cycle makes *R. marginata* an excellent model system to study evolution of eusociality.